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IMMATURE STAGES OF METALMARK MOTHS FROM THE GENUS *BRENTHIA* CLEMENS (CHOREUTIDAE): MORPHOLOGY AND LIFE HISTORY NOTES

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ABSTRACT. In this paper the immature stages of *Brentbia monolychna* Meyrick (Choreutidae: Brenthiinae), as well as their ultrastructure, are described and figured. This is the first description of a New World brenthiine. In addition, notes on life history for four New World species of *Brentbia* Clemens are provided, including mention of their host plants and parasitoids. Host plant utilization of the genus is discussed. A clarification of the nomenclature of the longest seta on the larval abdominal segment 9 is proposed. Earlier literature disagrees on whether this is a lateral, subdorsal, or dorsal seta – my examination suggests it is the subdorsal seta 1. The recorded distribution of *Brentbia pavonacella* Clemens is questioned, and a revised distribution is suggested. Moreover, an escape mechanism, employed by all known *Brentbia* larvae, is discussed. Finally, a list of morphological and behavioral synapomorphies for the subfamily Brenthiinae and the genus *Brentbia* is provided.

Additional key words: Microlepidoptera, chaetotaxy, ultrastructure, larval escape behavior, parasitoids, Braconidae

Brentbia Clemens is a cosmopolitan genus of metalmark moths (Choreutidae). With more than 80 described species and likely an even greater number of undescribed species (Rota 2003), it is among the largest microlepidopteran genera. Together with the genus *Litobreuthia* Diakonoff, *Brentbia* is classified in the subfamily Brenthiinae (Heppner and Duckworth 1981). The relationship of brenthiines to the other two choreutid subfamilies, Choreutinae and Millieriinae, is under study (J. Rota in prep.).

Moths in the genus *Brentbia* are small – wing size ranges from 6 to 14 mm. With blue or violet metallic and white markings on dark backgrounds, wings of most species look very similar (Figs. 1–3), so much so that genitalic dissections are often necessary to confirm identification. Adults of *Brentbia* mimic jumping spiders by holding their wings to the side and above the body, and moving in rapid, jerky motion (Robinson *et al.* 1994; Rota and Wagner 2006).

Life history information is available for only a few species, mostly from Asia (e.g., Arita 1987). *Brentbia* larvae appear to be relatively specialized, one species usually feeding on a single genus or closely related genera of plants (Arita 1987; Rota 2003). The larvae of known species are surface-feeding leaf skeletonizers (Arita 1987; Aiello and Solis 2003). All known larvae seem to have a similar predator/parasitoid avoidance

mechanism (see below; Williams 1951; Diakonoff 1986; Aiello and Solis 2003).

Immature stages of *Brentbia* have been described for a handful of species (e.g., Williams 1951; Arita 1987). In this paper, the larval and pupal stages of *Brentbia monolychna* Meyrick are described and figured. This is the first detailed description of the immature stages of a New World member of the subfamily. In addition, life history notes are provided on *B. monolychna*, as well as three of its congeners: *B. hexaselena* Meyrick, *B. pavonacella* Clemens, and *B. stimulans* Meyrick.

MATERIALS AND METHODS

Larvae of *B. monolychna*, *B. hexaselena*, and *B. stimulans* were collected from 2001 to 2004 in a tropical wet forest at La Selva Biological Station, a lowland reserve on the Atlantic slope of Costa Rica, Province of Heredia. *B. monolychna* pupae were reared from a collection of larvae in August 2004 also from La Selva. *B. pavonacella* larvae were collected on September 8, 2002, in Illinois, Coles County, Fox Ridge State Park, by Terry L. Harrison. Rearing was done in a laboratory in plastic bags or plastic vials filled with foliage and some soft paper tissue for control of humidity. Periods of light and dark corresponded to natural light cycles.

For preservation, larvae and pupae were placed into nearly boiling water for less than a minute and then

transferred to 75% ethanol (Zimmerman 1978). Specimens for viewing in the SEM were dehydrated in a graded ethanol series (ending in 100%), transferred to fresh solutions of hexamethyldisilazane three times, each time for approximately 15 minutes, and then immersed into fresh hexamethyldisilazane and allowed to air-dry. Dried specimens were sputter coated with gold/palladium.

A LEO/Zeiss DSM 982 Gemini Field Emission SEM was used. Photographs of adults and larvae were taken with a Nikon D100 and D1. The pupal photograph was taken with a digital camera attached to a Leica microscope, connected to a computer with Automontage® software (Synoptics Ltd., Cambridge, UK). Line art was prepared with a camera lucida. All images were edited in Adobe Photoshop CS®.

Measurements were made using an ocular micrometer. Chaetotaxy nomenclature follows Hinton (1946) and Stehr (1987). Usage of other terms is as defined in the Torre-Bueno Glossary of Entomology (Nichols 1989). Larval description is based on the last instar. Voucher specimens are deposited in the University of Connecticut Entomological Collection (UCMS).

RESULTS

Host plants. Larvae were collected and reared on the following host plants: *B. hexaselena* larvae from *Byttneria aculeata* (Jacq.) Jacq. (Sterculiaceae) (Fig. 4); *B. monolychna* larvae from *Calathea crotalifera* S. Watson (Marantaceae), other *Calathea* spp., and from *Heliconia* sp. (Heliconiaceae) (Figs. 5–10); *B. stimulans* larvae from *Cecropia insignis* Liebm. (Cecropiaceae); and *B. pavonacella* larvae from *Desmodium glutinosum* (Muhl.) Wood (Fabaceae) and other *Desmodium* spp. (Figs. 11–12).

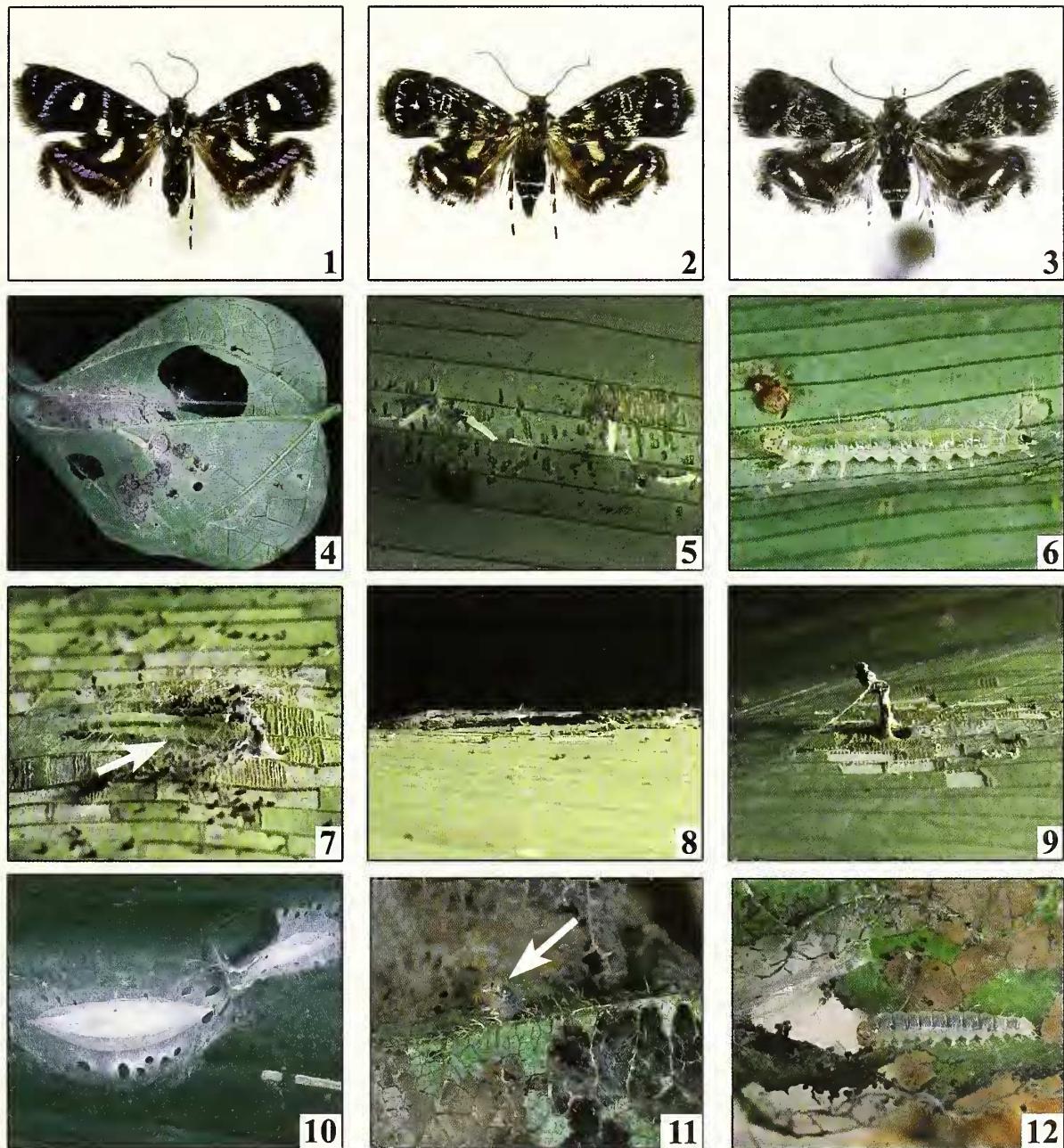
Morphology of the immature stages of *Brenthia monolychna* Meyrick, 1915. *Larva.* Pale green in life (early instars almost white) (Figs. 5–7), translucent, without any patterning on thorax and abdomen, and with long setae; average length 8.5 mm (n=5). Only primary setae present. *Head.* With dark brown spots (Fig. 6), widest at about level of P1; vertex only shallowly concave; hypognathous; setae as in Figs. 13–15; A3, AF1, and P1 extremely elongate, approaching length of head; A3 three times as long as A1, and A1 and A2 subequal; AF1 five to six times as long as AF2; S2 posteriad of stemma 1; spinneret well developed, more than twice as long as labial palpus, slender (Figs. 15, 16); stemma VI highly reduced; other stemmata arranged in a semicircle, with stemma 2 positioned slightly outside of semicircle (Fig. 14); frontoclypeus extending half way to epicranial notch; labrum notched, with toothed underside (Figs. 17, 18); mandible with well-developed teeth; hypopharyngeal spines prominent (Figs. 19, 20). *Thorax.* D1 and D2 subequal; T1 with L1 three times as long as L2 and L3, SV bisetose; T2 with L1 two times as long as L2 and three times as long as L3; T2 and T3 with SV unisetose, SD1 and SD2 subequal, L setae on separate pinacula. *Abdomen.* Setae very long, especially posteriad (Fig. 31); D1 and D2 subequal, L1 longer than L2 and L3; A1–2 and A7–9 with SV group numbering 3:3 and 2:2:1, respectively; A1 with L setae on separate pinacula; A2 with SV setae in triangle; A8 with setae D1 and D2 on common middorsal pinaculum; A9 with D1, SD1, L1, and L2 on common subdorsal pinaculum, with

D1 and D2 in vertical alignment, and with extremely long SD1, corresponding in length to 4–5 abdominal segments. Prolegs long and slender, subcylindrical (Fig. 21); crochets uniserial and uniorbital; A3–6 with approximately 12 crochets arranged in mesal pennellipse (Fig. 22); A10 with 16 crochets in semicircle with posterior gap.

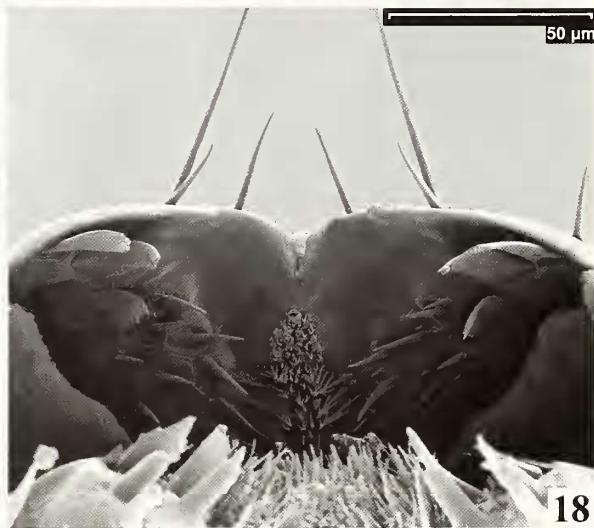
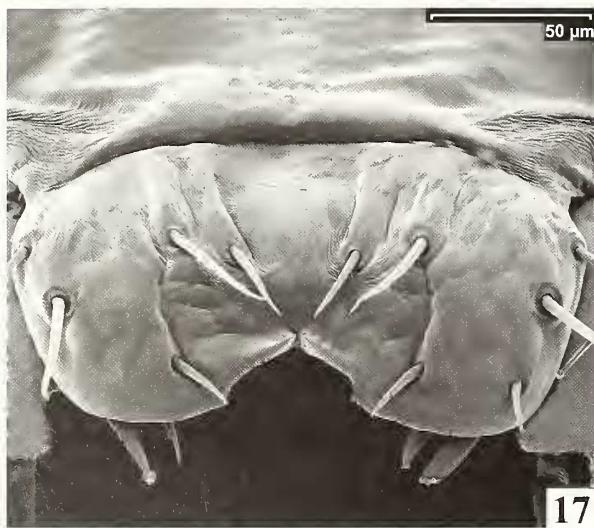
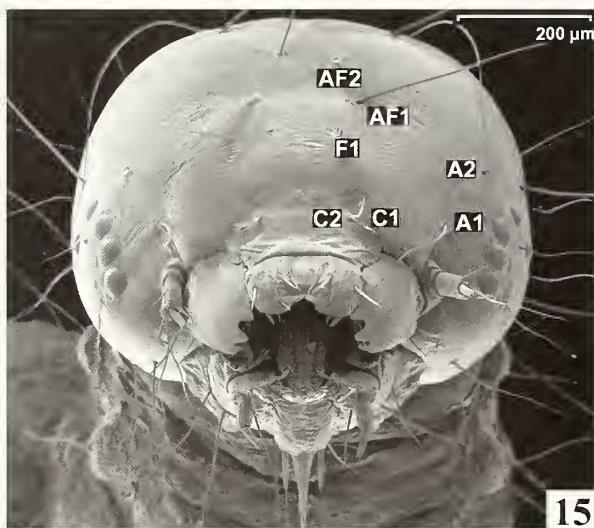
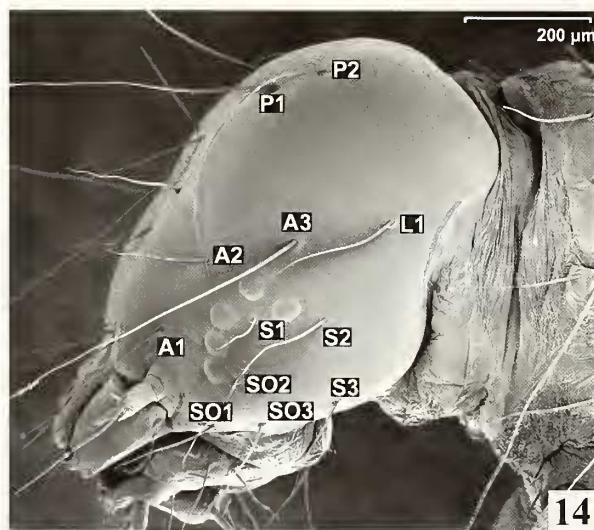
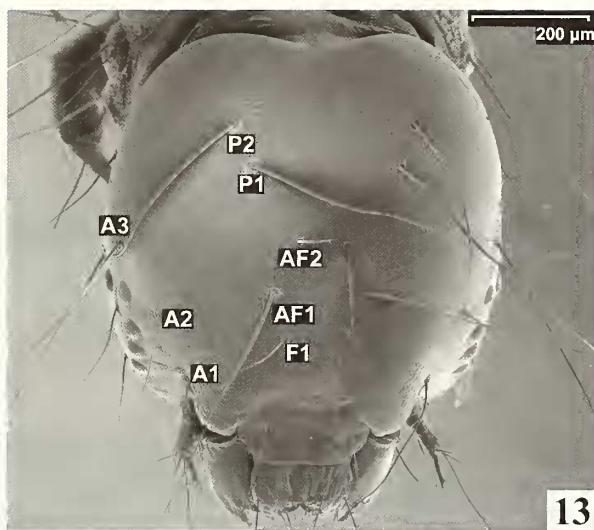
Pupa. Average length 6.25 mm (n=3); with long, fork-tipped setae (Figs. 29, 32), and short, thickly arranged, caudally oriented dorsal spines on A4–8; A4 with dorsal spines poorly developed (Fig. 23), A5 spines larger than on A4, but smaller than on A6 or A7 (Fig. 24), A6–A7 spines well developed (Figs. 25–27), A8 with field of poorly developed spines (Fig. 28). Cremaster on A10 with two pairs of slightly curved slender spines, two pairs of hook-tipped setae three times as long as spines, and two pairs of very long fork-tipped setae six to seven times as long as hooks (Figs. 29, 30).

Life history notes. As in other choreutids, larvae of *Brenthia* leave diagnostic feeding damage: superficial skeletonization of undersides of leaves (Figs. 4–7). While earlier instars often feed in groups (Fig. 5), older larvae are normally solitary (Figs. 6, 7). Over the feeding area larvae create a thin, loose web into which they incorporate fecal pellets (Figs. 7, 8). Most likely, the incorporation of fecal pellets is not an active process; rather, it happens passively as the caterpillars move about the shelter and their feculae accumulate in the webbing. Larvae of all four *Brenthia* species that I have observed chew a roughly circular “escape hatch” – a wormhole – somewhere in their feeding shelter. When resting, they sit with their head next to the hole. If disturbed, larvae dash through the wormhole to the other side of the leaf (Figs. 7, 9, 11). After a little while, they wriggle through the opening backwards to their original position. Larvae of some species (e.g., *B. monolychna*) construct “fecal stalactites” (Aiello and Solis 2003) in their feeding area (Fig. 9). Located at the mouth of the escape hole on the leaf underside, these structures appear to serve as landmarks that facilitate the quick escape of a larva (see Aiello and Solis 2003). The fecal stalactites also seem to serve to suspend the webbing above the larva. *Brenthia* cocoons are often spun on the leaf undersides or somewhere on the stem and are composed of two principal parts: an inner one, which is white, fusiform, and composed of multiple layers of thick silk; and a thin, outermost silken layer that forms a sheet over the cocoon proper (Fig. 10). The whole cocoon of *B. monolychna* is less than 2 cm along its longest axis. The pupa is protruded from the cocoon at eclosion. For all four species, the development from the pupa to the adult stage took about ten days.

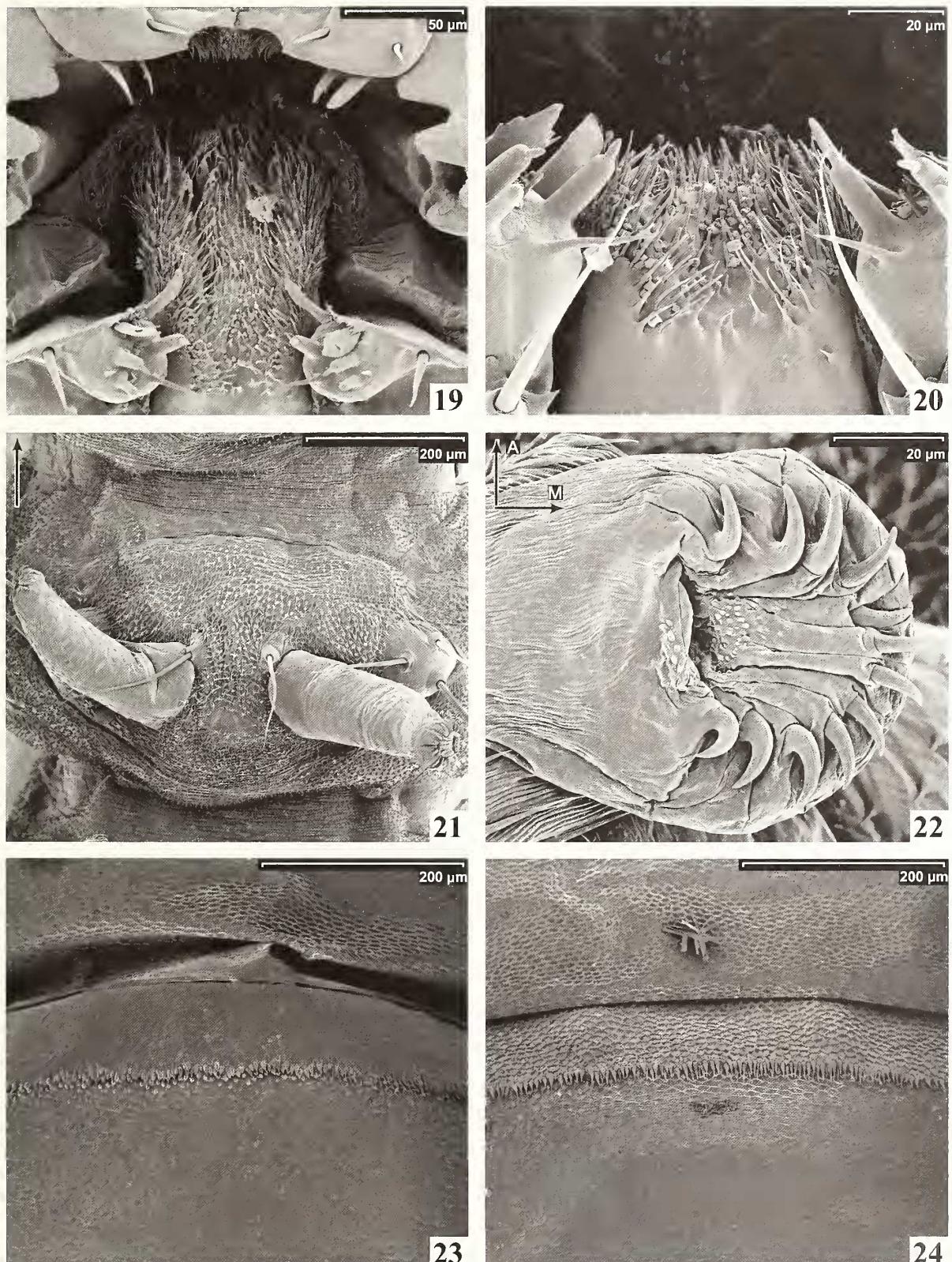
Larvae of the three *Brenthia* species reared from La Selva are heavily parasitized by braconid wasps (Hymenoptera: Braconidae) (Table 1 and Fig. 10). In *B. monolychna* the parasitism rate is close to 85% (n_{larvae}=51). In *B. hexaselena* (n_{larvae}=5) the rate is about 20%, and in *B. stimulans* (n_{larvae}=4) about 50%, but note small sample sizes. I have not reared any parasitoids from *B. pavonacella* (n_{larvae}=25).



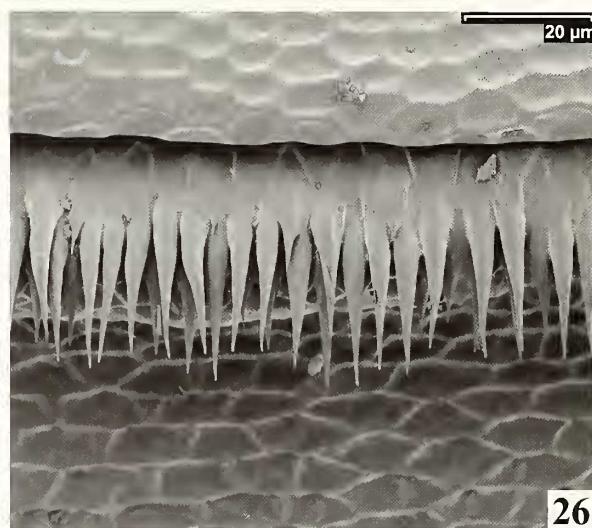
Figs. 1-12. 1. *B. hexaselena* adult. 2. *B. monolychna* adult. 3. *B. pavonacella* adult. 4. *B. hexaselena* larva on its host plant. *B. monolychna*; 5. Gregarious feeding of young larvae; 6. Last instar larva; 7. Larva going through an escape hatch; 8. Larval webbing; 9. Fecal stalactite; 10. Cocoons of a healthy larva (center) and of a parasitized larva (upper right). *B. pavonacella*; 11. Larva going through an escape hatch; 12. Last instar larva.



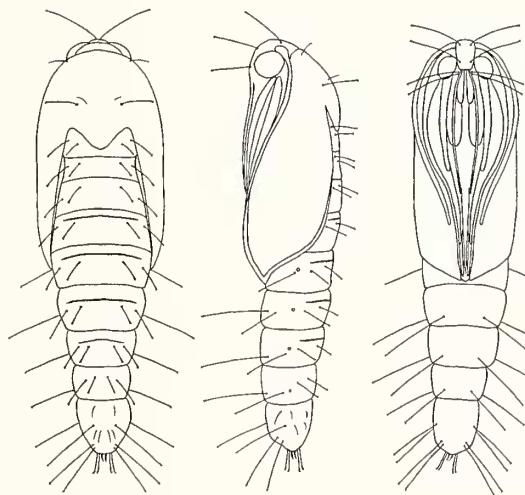
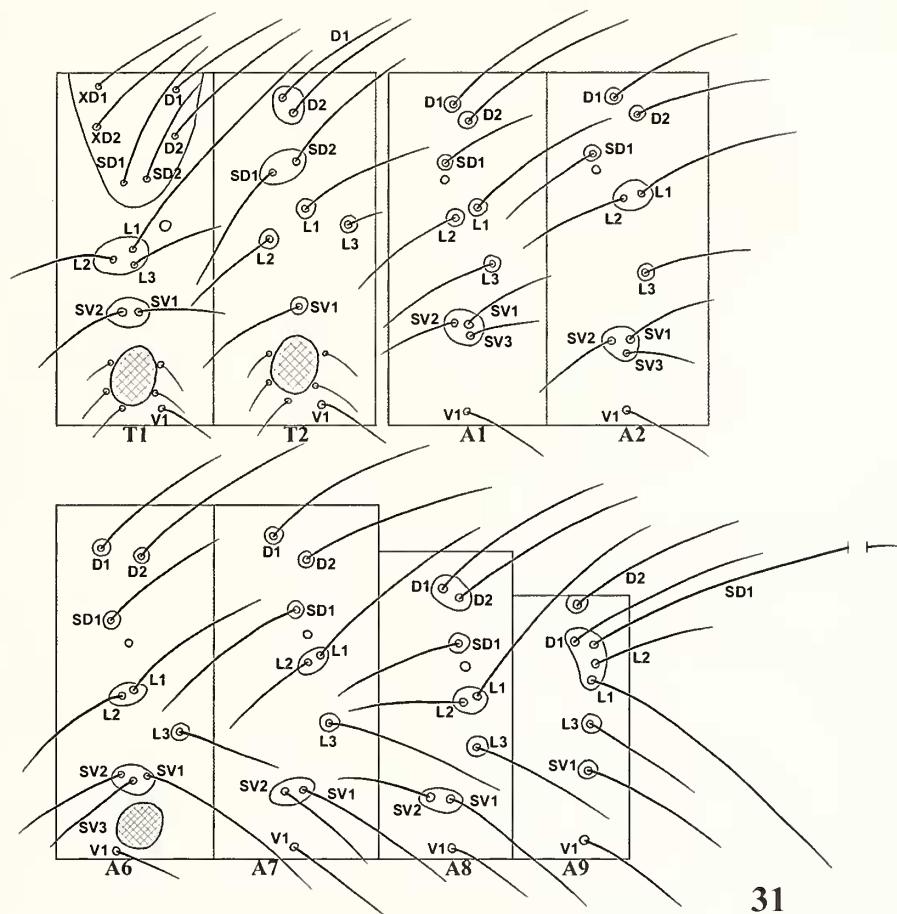
FIGS. 13–18. *B. monolychna* larva: 13. Head, dorsal; 14. Head, lateral; 15. Head, frontal; 16. Head, ventral; 17. Labrum, dorsal; 18. Labrum, ventral.



FIGS. 19–24. *B. monolychna* larva: **19 and 20.** Hypopharyngeal spines; **21.** Ventral view of abdominal prolegs (arrow points to anterior); **22.** Crochets on an abdominal proleg (arrows pointing A: anterior and M: mesad). Pupa: **23.** Dorsal spines on A4; **24.** Dorsal spines on A5.



Figs. 25–30. *B. monolychna* pupa: **25**. Dorsal spines on A6; **26**. Close-up of dorsal spines on A6; **27**. Dorsal spines on A7; **28**. Poorly developed field of dorsal spines on A8; **29**. Dorsal view of the cremaster; **30**. Close-up of the cremaster.



FIGS. 31-33. *B. monolychna*: 31. Larval chaetotaxy; 32. Pupa, dorsal, lateral, and ventral view. *B. pavonacella*: 33. pupa.

B. monolychna is an unusually abundant species at La Selva Biological Station, at least as a larva—there were traces of larval feeding damage on almost every host plant examined ($n > 300$). The adult can be seen during the day on vegetation in the vicinity of its host plant; occasionally adults also come to mercury vapor light.

B. hexaselena is uncommon in collections from La Selva, but it can be frequently encountered during the day around stands of its host plant. I have never seen it come to lights at night (number of blacklighting nights at La Selva *ca.* 100).

B. stimulans appears to feed on mature *Cecropia insignis* plants only—I examined dozens of saplings and never found any signs of larvae or their feeding damage. This species, most likely because its host plant is a tall tree, is rarely encountered.

Brenthia pavonacella is the only member of the genus found in North America north of Mexico (Hodges *et al.* 1983). It is widely distributed in the eastern United States, north to southern New York (Forbes 1923). *B. pavonacella* is often common where found. Like *B. hexaselena* and *monolychna*, it is principally diurnal.

DISCUSSION

In larvae of *Brenthia*, the longest seta on A9 is considered under different names by different authors: Arita (1987) refers to it as an additional seta of the L-group, whereas Heppner and Duckworth (1981) call it D2. Based on a careful examination of setal arrangement on all the abdominal segments and comparisons with Hinton (1946) and Stehr (1987), I agree with Williams (1951), who designated this seta as SD1.

Forbes (1923) characterized the distribution of *B. pavonacella* as extending from New York southward to Brazil. This is almost certainly incorrect. Throughout the Neotropics there are many species of *Brenthia* with wing patterns very similar to that of *pavonacella*. My examination of genitalic characters and molecular data suggests that many superficially similar species often prove to be distantly related (Rota unpublished data). *Brenthia* collections at INBio¹ (for Costa Rica) suggest there are at least 10 species in the country, most of which are undescribed, and none of which is assignable to *pavonacella*. Further evidence supporting this revision of the species' distribution is that *B. pavonacella* larvae are strictly limited to *Desmodium* in North America, and no Neotropical *Brenthia* have been reared from plants in this genus.

All known *Brenthia* larvae exhibit a similar escape behavior involving escaping through wormholes chewed

TABLE 1. Genera of braconid parasitoids from *B. monolychna* and *B. hexaselena*

<i>B. hexaselena</i>	Microgastrinae
	<i>Dolichogenidea</i> Viereck
<i>B. monolychna</i>	Microgastrinae
	<i>Dolichogenidea</i> Viereck
	Agathidinae
	<i>Plesiocelus</i> van Achterberg
	Orgilinae
	<i>Orgilus</i> Haliday

into the floor of their feeding shelter (Aiello and Solis 2003; Williams 1951; Diakonoff 1986; this paper). While clearly this represents a predator/parasitoid escape mechanism, it is also evident that this behavior is not especially successful for avoiding parasitism by braconid wasps—as noted above, parasitism rates were as high as 55% in *B. monolychna*.

Most species of *Brenthia* appear to be specialists—they feed on a single genus of plants or closely related groups of plants. Yet, when taking a look at the whole genus, *Brenthia* species have been recorded from a rather extraordinary array of unrelated plant families that includes both monocots and dicots: Boraginaceae (Williams 1951), Cecropiaceae (LaPierre pers. comm.; this paper), Asteraceae, Dipterocarpaceae, Euphorbiaceae (Robinson *et al.* 2007), Fabaceae (Arita 1987; Aiello and Solis 2003), Heliconiaceae (this paper), Malvaceae (Heppner 1985), Marantaceae (Aiello and Solis 2003), Moraceae (Robinson *et al.* 2007), Sapindaceae (Heppner 1985), Sterculiaceae (Hespenheide pers. comm.; this paper), Tiliaceae (Robinson *et al.* 2007), and Urticaceae (Diakonoff 1986; Arita 1987). There are also unconfirmed records of rearings from ferns (specimens in Costa Rica's INBio collection). A species-level phylogeny of the genus, at this point unattainable, would create an opportunity for the study of the evolution of *Brenthia*'s remarkable ability to exploit novel and, evidently, unrelated host plants.

A review of literature describing immature stages of 12 choreutid genera (*Brenthia* from Arita (1987), Williams (1951), and this paper; *Litobrenthia*, *Anthophila*, *Choreutis*, *Prochoreutis*, *Saptha*, and *Tebenna* from Arita (1987); pupae of *Anthophila*, *Choreutis*, *Prochoreutis*, and *Tebenna* from Patočka (1999); *Asterivora* from Dugdale (1979); *Rhobonda* and *Zodia* from Rota (2005); *Caloreas* from Keifer (1937); *Tortyra* from Wille (1937)), as well as my own investigation (unpublished data for *Choreutis*, *Hemerophila*, *Prochoreutis*, *Tebenna*, and *Tortyra*), suggest the following character states as synapomorphies

¹INBio – Instituto Nacional de Biodiversidad

for the subfamily Brenthiinae: 1) hypognathous head (semiprognathous in Choreutinae); 2) extremely long SD1 seta on A9 (SD1 length similar to L setae in Choreutinae); 3) A9 with D1 seta present (D1 absent in Choreutinae); and 4) crochets in an incomplete circle (complete circle in Choreutinae). Likewise, the immatures of choreutine genera share numerous synapomorphies (Rota unpublished data). Together with preliminary molecular data (Rota unpublished data), these different sets of shared derived characters for Brenthiinae and Choreutinae strongly suggest that both subfamilies are monophyletic, contra Dugdale *et al.* (1998) and in agreement with Heppner and Duckworth (1981).

Character states that appear to be synapomorphies for the genus *Brenthia* are 1) crochets in a mesal pennellipse (semicircle in *Litobrenthia*), 2) two SV setae on A8 (one SV seta in *Litobrenthia* and choreutine genera except *Rhobonda*), 3) larval escape behavior through a previously made hatch, 4) two pairs of curved spines in the pupal cremaster, and 5) long forked setae on the pupa. Characters 3), 4), and 5) were not discussed in the only published description of *Litobrenthia* (Arita 1987), so at this point it is impossible to say whether these characters, or a subset of them, will prove to be synapomorphic for *Brenthia* or are in fact synapomorphies for Brenthiinae. More work is needed, especially in the Neotropics where *Brenthia* appears to be highly diverse, before we can begin answering these and other questions about this fascinating group.

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